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THE EFFECT OF RHYTHMIC SOUND SIGNALS ON THE CRICKET FLIGHT SYSTEM

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INTRODUCTION

As is true of many other insects, crickets can localize a sound source during flight. Recently much attention has been paid to cricket phonotaxis during tethered flight (e.g. Moiseff et al., 1978; Nolen and Hoy, 1986). Investigations of neuronal networks controlling wing muscles of crickets have also been conducted (Robertson, 1987; Hennig, 1990). Wing beats of flying insects are accompanied by cuticular vibrations and sound, which one can consider to be noise preventing perception and analysis of acoustical signals. Thus, a question arises about mechanisms which diminish the negative effects of noise, or in other words, about the functional interaction between the auditory system and the neuronal network which controls flight. In this paper, the results of an investigation of the influence of rhythmic sound signals on the cricket flight system are described.

METHOD

Female crickets (age of 2-4 days after the last molt) were used in the experiments) A wire (diameter 0.2 mm, length 30 mm) was attached by wax to the pronotum of a cricket. The other end of the wire was connected rigidly to a piezoelectric vibrosensor. The output electrical signal, transformed into an impulse form (I) corresponded to rhythmic thorax oscillations at the beginning of the down-stroke of the wings. The temporal relation between the impulses and wing position were recorded by means of stroboscopic photography. The stimulating acoustical signal was formed by means of a special generator constructed in the laboratory.

RESULTS AND DISCUSSION

The period of the wing strokes (T) in female crickets is highly stable. The average value of T is 39 ±2 ms. The impulses were binned and stored in relation to the input stimuli (PSTH) was carried out during acoustic stimulation by the calling song (Fig. 1).

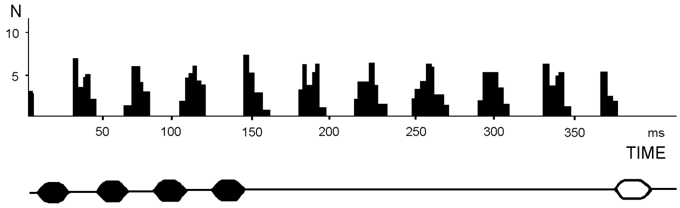

Fig. 1. Post-stimulus time histogram (PSTH) of wing beats (downstrokes) during synchronization of the flight rhythm with acoustic stimuli. Bin width - 4 ms, spike data collected during 6 s. The stimulus, a chirp of a synthetic male calling song is shown below the histogram.

The flight rhythm was found to be "temporally coupled" to the sound rhythm. To investigate this effect in detail we used the method of string decomposition of the rhythmic process, the beginning and the end of each string being coincident in time with the beginning of the periodic stimulus. Figure 2A illustrates the process of synchronization and desynchronization of the flight rhythm during sound stimulation. In this case each phase line can be divided into three parts: 1-2, linear increase of stroke period (T); 2-3, synchronization (phase shift in the range of 1/4 of the period T); and 3-4, desynchronization. This sequence in the restructuring of the flight rhythm is the most typical effect and is observed in all experimental insects. The results in interval 1-2 are described best by a parabolic function. This observation will be clearer if we construct the second symmetric part of the process (interval 2-5). The transfer from point 2 to synchronization is not obligatory. A segment of a phase line without 'stimulus capture' of the stroke rhythm is shown in Fig. 2B.

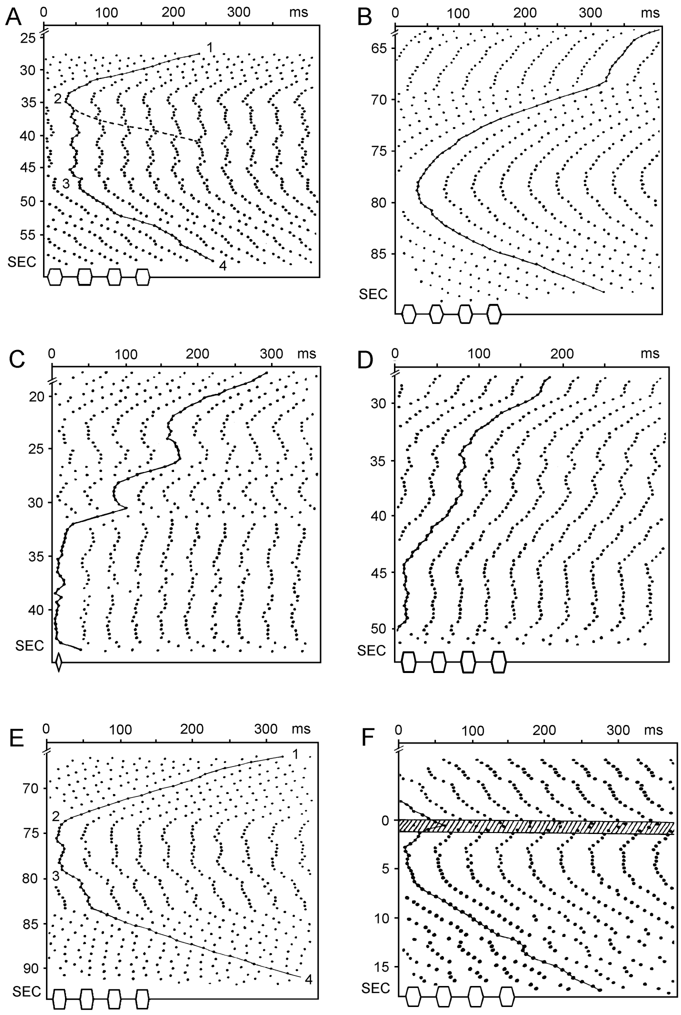

Fig.2. Effect of acoustic stimuli on the flight pattern. Horizontally adjacent points display wingbeats (hind wings at the beginning of downstroke). 1-5 points on the phase line. The stimuli are shown below the figures. Shaded stripe indicates time when SPL increased from 30 to 40 dB.

It can be noted that the stroke period (38 ms) in the section 2-3 (Fig. 2A) is not equal to the period of pulse repetition (44 ms). This effect was typical for all experimental females. One can drow the conclusion that the tuning of the motor pattern occured in response to the chirp as a whole. To check this suggestion, we stimulated females with single pulses with a duration of 6, 20 or 80 ms and a repetition period from 320 to 360 ms. An example of a flight pattern synchronization with a train of single pulses (6 ms) is shown in Fig. 2C.

The phase curve in section 3-4 (Fig. 2A) which reflects a desynchronizing process, has specific bends due to irregularity in the phase change. This effect is shown more obviously in Fig. 2E, where short repetitive capture of the stroke rhythm by the acoustical stimulus occurs. The tendency to change the period T after a desynchronization can be different even in one insect. As is shown in Fig. 2D, synchronization takes place twice.

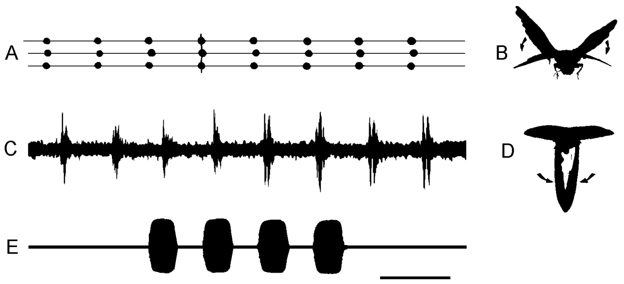

Fig. 3. Relationship between movements of hindwings and noise pulses. A: Horizontally adjacent points indicate the beginning of hindwings downstroke (B) C: Noise pulses are produced by hindwings at the end of downstroke (D). E: The acoustical stimulus - synthetic calling song. B and D - stroboscopic photographs. Time scale 50 ms.

In general a multiple synchronization of the rhythm can occur in the course of stimulus action. It is likely that continuous confirmation is required to support flight system activity synchronized with an acoustic stimulus. Let us suppose that a flying female perceives a conspecific signal and turns towards its source. Then the amplitude of sound will rise rapidly as the distance between the female and the calling male decreases. It is possible that this effect is responsible for maintaining synchronization.

We carried out experiments specifically designed to check this suggestion. A model of the calling song was presented to females and then the amplitude of the signal was increased by 10 dB monotonically over a 1.5 s interval. An increase in amplitude of more than 30 dB resulted in synchronization (Fig. 2F).

The reader may note than the threshold for onset of synchronization (30-35 dB) is low, especially in view of the fact that a flying female produces an easily audible sound which occurs at the moment the hind wings meet in the terminal low position (Fig. 3).

The envelope of this sound is a 'pulse' with pronounced noise components and a duration of 1/6-1/4 T. The spectrum of the noise is almost linear over the whole range of measurement (1-70 kHz). The beginning of the pulse has a delay equal to 1/4-1/3 T in relation to the first impulse I. The noise appears concurrently with supination of the wing and has an amplitude of about 45-50 dB near the auditory organ of the cricket.

The mutual time relationship between the stimulating sound and the noise pulses when the flight rhythm is synchronized allows us to suggest that the female tries to extract the initial phase of the rhythmic signal from the noise, which can be considered as 'a time reference point' for further analysis of the chirp. It is clear in this case how the female can extract a useful signal from continuous rhythmic noise, which is about 10-20 dB above the signals.

Furthermore, we can suggest that there must be neuronal connections between the flight neurons and the auditory system necessary to suppress responses to the broad band noise which appears simultaneously with the wing movements.

In theory, there are three possible basic mechanisms of synchronization: 1) reflective stroke right after the occurence of the acoustical stimulus; 2) delaying the next stroke up to the moment that the sound arrives; and 3) an adjustment of the stroke period T by means of a special compensatory system. A corresponding shortening or prolongation of the flight cycle must occur, which coincides in time with the onset of the stimulus. Stable synchronization is impossible due to the limited possibilities of such variations. In both cases, phase lines must be dramatically different in form before and after the beginning of the stimulus. There are no essential differences in Fig. 2, and this indicates that there is the special compensator system which makes smooth variations in the period T.

Investigation of phonotaxis in the flying cricket shows that acoustic information is used actively for flight control. Our data indicate that this information exerts an influence on the rhythmic activity of the flight system. Analysis of the data obtained can define at least three features of such influence: 1. The auditory system must have a mechanism to extract the time interval corresponding to the repetition period of the chirp. A study of Wiese and Albrecht (1990) indicates tuning of certain auditory interneurons to this interval. 2. The motor system itself cannot perform the extraction of this rhythm, because its main period is substantially shorter than the repetition period of chirps. 3. The weak dependence of phase tuning in the motor system on the sound stimulus structure (the number of pulses and stimulus duration) suggests that the commands from the auditory system are concerned with the beginning of the first pulse in a chirp.

We conclude that a detailed study of diagrams which show synchronization permits some conclusions to be drawn about the morphofunctional organization of the flight pattern generator itself. Thus auditory signals can be used as natural stimuli to test a motor system and model of it. Our approach may be useful for understanding other problems concerned with the effect of fast exogenous rhythms on endogenous rhythmic processes in the nervous system.

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